

Territorial Hilltopping Behavior of Three Swallowtail Butterflies (Lepidoptera, Papilionidae) in Western Brazil.

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Abstract. This paper investigates differences in the territorial hilltopping behavior of *Papilio thoas*, *Battus polydamas* and *Eurytides orthosilaus*. Seven behavioral activities of hilltopping males are described and measured, including inter and intraspecific aggression, territory establishment, and choice of preferred sites for territories. *P. thoas* and *B. polydamas* shared many behavioral characteristics and preferred the same territorial site, near the highest point of the hill. Most interspecific aggression occurred between these species. *P. thoas*, the dominant species, won aggressive encounters and established its territories first. *B. polydamas* set up territories in neighboring areas placed around the territories of *P. thoas*. Marked behavioral differences were found between *E. orthosilaus* and the other species; its territories were established several meters above the largest trees in the area and did not overlap with those of *P. thoas* and *B. polydamas*. Behavioral activities in these butterflies occurred in a sequential pattern each day. Aggressive acts predominated in the early hours and decreased as territory owners become established and newly arriving butterflies become rare.

Introduction

Many butterflies and other insects fly to hilltops in order to mate (Shields, 1967; Baker, 1983). Hilltopping is in many aspects similar to lek behavior shown by many birds and other vertebrate species. It is believed to increase the mating efficiency of individuals of a species reducing the area in which sexual encounters can occur (Poulton, 1904).

According to Alcock (1987) it is not obvious why hilltops would become "rendezvous points" for any species. It has been noted that these sites generally do not contain food resources for adult butterflies, nor are they locations where females emerge, oviposit or even rest. There are only males waiting to mate.

Hilltopping butterflies exhibit a considerable diversity with respect to the way that males aggregate and form territories (Courtney & Anderson, 1986). In some species males form clusters of several individuals with little or no aggressive behavior among them (see examples in Alcock, 1985; Baughman et al., 1988). In the other extreme males do not tolerate each other, and form mating territories as defined by Brown & Orians (1970); such is the case for many swallowtail butterflies (Shields, 1967; Lederhouse, 1982; Rutowski et al., 1989).

Although much information has been obtained on hilltopping behavior, it is still poorly documented which species exhibit such behavior, especially in the tropics. In this paper I examine some aspects of the territorial hilltopping of males of three large swallowtail butterflies that use the same place for hilltopping: *Papilio thoas brasiliensis* Roths. & Jord., 1906, *Battus polydamas polydamas* (L., 1758) and *Eurytides orthosilaus* (Weymer, 1899). I describe their preferences of sites for territories and use a behavioral method to estimate and compare the frequencies of different kinds of behaviors associated with hilltopping, including inter and intraspecific encounters and other behaviors associated with territory establishment. The order of occurrence of determined behavioral activities of males is also reported.

Study Site and Methods

Field work was done in the region of the Rio Manso, Mato Grosso State, western Brazil (55°50'W, 14°52'S) on sunny days between May 16-21 and October 13-16, 1988; and April 22-26, 1989. Observations and data collecting were concentrated on the top of the highest hill in the area (405 m elevation), composed of a dome measuring 120 x 40 m covered with a combination of cerrado vegetation, grasses and bare rocks. Forest vegetation is found 150 m below at the bottom of two small valleys around the

Table 1. Behavioral categories performed by males of *P. thoas*, *B. polydamas* and *E. orthosilaus* during territorial hilltopping and their characteristics (see also the text).

Category	Species	Characteristics
Intraspecific Aggression	All	Includes chasing, grappling in the air and falling to the ground
Interspecific Aggression	All	Only chasing, usually faster than intraspecific aggression
Extensive Patrolling	All	An exploratory flight over a large area of the hilltop
Restricted Patrolling	All	Flying about inside a small and well defined area
Perching	All but <i>E. orthosilaus</i>	Resting on some vantage point the male darts out at every passing butterfly
Hovering	All	Hovering or gliding in place
Flying in circles	Only <i>P. thoas</i>	Flying in perfect circles within a diameter of 2 m

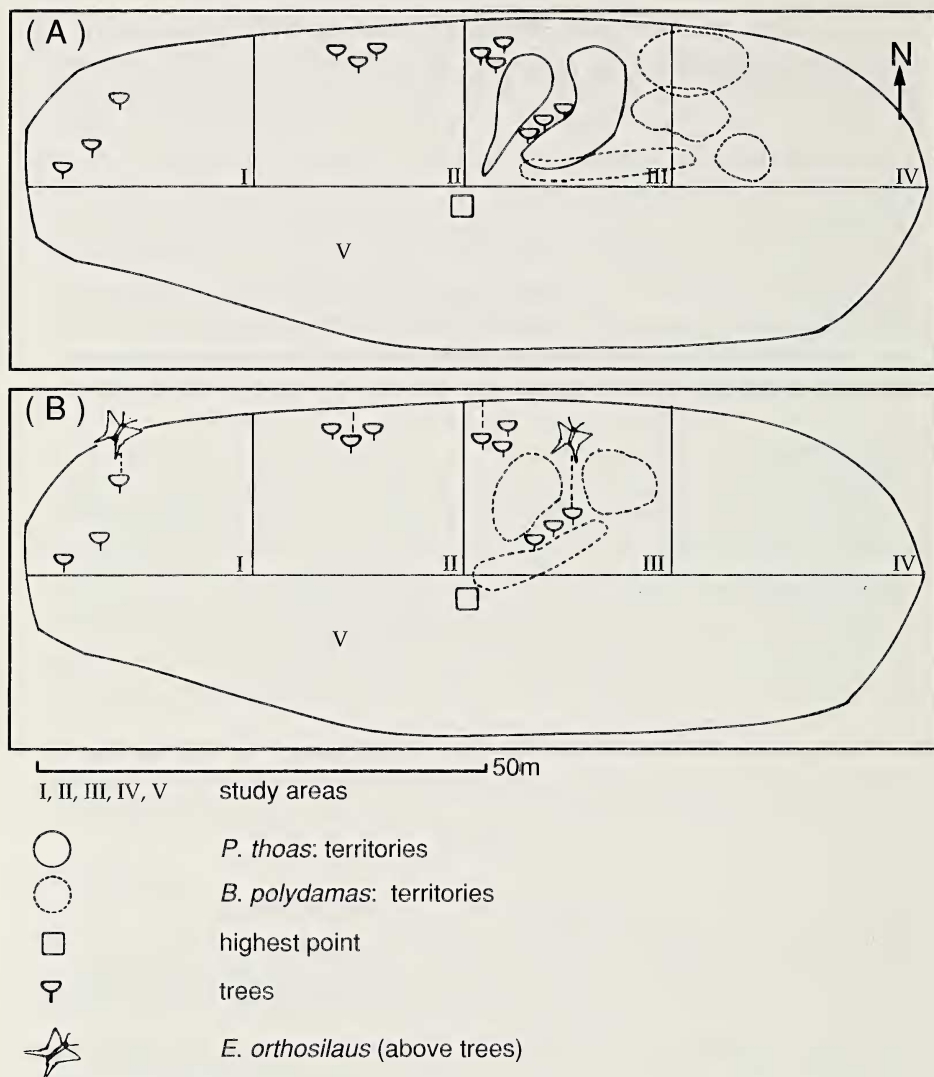


Fig 1. Preferred sites for territories. (A) Territories of *P. thoas*, near the highest point, and of *B. polydamas*, when both species occur together. (B) Territories of *B. polydamas*, near the highest point, after remotion of males of *P. thoas*. Territory boundaries fit displacements done during "restricted patrolling".

north side of the hill. Several other species of butterflies, skippers and bees were also observed using this place for hilltopping.

Behavioral activities were categorized based on aggressivity and individual displacement over the area (Table 1). Records of behavioral categories were taken at the end of the rainy season (April). A scan method (Altmann, 1974) was used for quantifying frequencies of behavioral categories. The instantaneous activities of butterflies were recorded every 5 minutes throughout the hilltopping period.

During scan intervals butterfly displacements were also recorded by six previously trained observers placed at special points of the hilltop. With this larger number of observers it was possible to follow butterflies individually for long periods of time. Preferred sites for territories were determined by the number of inter and intraspecific aggressive encounters in different areas of the study site (Fig. 1).

Results

HILLTOPPING

Hilltopping is concentrated in the warmer periods of the day. Males generally appear on the hilltop between 0900-1130 AM depending on the time of the year and temperature of the day and can remain there for more than three hours. Territorial hilltopping was only observed after the rainy season (April and May) when there was a relatively greater number of butterflies on the hilltop and aggressive encounters among individuals were frequent. In October 13-16 the number of butterflies present on the hilltop was small and males did not form territories.

BEHAVIORAL DIFFERENCES AMONG SPECIES

Differences in the kinds and frequencies of behavioral categories performed by males of each species during territorial hilltopping are shown in Table 2. The maximum number of butterflies on the hilltop recorded during scan sampling and the number of established territories was 3/2 for *P. thoas*, 5/4 for *B. polydamas* and 5/3 for *E. orthosilaus*.

P. thoas and *B. polydamas* shared a larger number of behavioral categories and showed a more diversified behavior than *E. orthosilaus*, who do not use "perching" and "flying in circles" behaviors. The latter was also not observed in *B. polydamas*. The most common behaviors shown by *P. thoas* and *E. orthosilaus* were extensive and restricted patrolling, and hovering by *B. polydamas*.

Nearly 25% of all behavioral records of *P. thoas* and *B. polydamas* and 15% of *E. orthosilaus* were related to aggressive encounters. In all cases these encounters were more frequent among conspecific males than between species (see Table 3).

More subtle differences among species also occurred within each behavioral category. Aggressive acts among conspecific males of *E. orthosilaus* can follow a standard sequence, always starting with horizontal or vertical chasing among two or more males and can last several minutes, sometimes ending very far from the hilltop. Chasing generally stops when one of the males flies away from the other or from the hilltopping arena. Chases usually determine territory owners. However, in some cases chasing can be followed by grappling in the air and falling to the ground. Depending upon the height and the place of the fall, serious wing damage can result. The butterflies hold each other with the legs and even with the clasper used by males to hold females during copulation. Grappling and falling were also seen in *P. thoas*, but more rarely than in *E. orthosilaus*, and never in *B. polydamas*.

Table 2. Relative frequency of behavioral categories performed by males *P. thoas*, *B. polydamas* and *E. orthosilaus* throughout a territorial hilltopping day in April, in the Rio Manso, Western Brazil (records were taken at five minute intervals; n= number of records)

Behavioral categories	<i>Papilio thoas</i> (n=62)	<i>Battus polydamas</i> (n=61)	<i>Euritides</i> <i>orthosilaus</i> (n=47)
Intraspecific Aggression	19.35	21.31	14.29
Interspecific Aggression	4.83	3.28	—
Extensive Patrolling	25.81	9.84	38.78
Restricted Patrolling	25.81	24.59	28.57
Perching	6.45	6.56	—
Hovering	9.68	34.43	18.37
Flying in circles	8.06	—	—

Table 3. Number of intra and interspecific aggressive encounters (AS and AO respectively) of *P. thoas*, *B. polydamas* and *E. orthosilaus* per area, during territorial hilltopping in the Rio Manso, Western Brazil

AREA	<i>P. thoas</i>		<i>B. polydamas</i>		<i>E. orthosilaus</i>	
	AS	AO	AS	AO	AS	AO
I,V	—	—	—	—	—	—
II	—	—	—	—	2	—
III	11	3*	2	2*	5	—
IV	—	—	3	—	—	—

* Interspecific encounters were between *P. thoas* and *B. polydamas*, except one case against a passing pierid butterfly

Extensive and restricted patrolling of males of *P. thoas* and *B. polydamas* occurred near the ground. Restricted patrolling is done over a very defined area that the animals cover repeatedly, following the same route. *E. orthosilaus* patrolled at higher elevations, near 5 m above the canopy of the large trees, and the routes followed were not repeated as in the other two species.

Activities related to feeding or oviposition by adult butterflies were never observed during any period of the year. Furthermore, hostplants of these species (*Piper* sp, for *P. thoas*, *Aristolochia* vines for *B. polydamas* and probably a Lauraceae used by *E. orthosilaus*) were not found among the local plants.

Mating success of these species seemed to be small given that matings were not observed. However, sometimes males of *E. orthosilaus*, when pursuing butterflies, possibly females, flew away from the hilltop without returning afterwards.

SEQUENTIAL PATTERNS OF BEHAVIORAL ACTIVITIES

The sequence in which males of all species showed each behavior and formed territories reveals that certain activities predominate at different times during hilltopping. Extensive patrolling is more common in newly arrived butterflies and before leaving the hilltop. During initial exploratory displacements other males were frequently encountered and aggressive acts occurred, characterizing an aggressive phase in the early hours. As territory owners became established and newly arriving butterflies became rare aggressive acts decreased.

After choosing a site for territory, males performed restricted patrolling for several minutes. Inside the area delimited by such behavior, which can be considered as the territory limits, males started to hover and perch (except for *E. orthosilaus*). Finally *P. thoas* began to fly in circles whereas *B. polydamas* and *E. orthosilaus* predominantly hovered.

TERRITORIAL SITES

The most desirable area for territory of each species as indicated by the number of aggressive encounters is shown in Table 3. *P. thoas* and *B. polydamas* preferred the same area (III) near the highest point of the hilltop. Most interspecific aggressive encounters occurred between these species, leading to the formation of nonoverlapping interspecific territories. *P. thoas*, the dominant species, often won these encounters and established its territory first. Under these conditions *B. polydamas* set up territories in neighboring areas placed around the territories of *P. thoas* (Fig. 1A). An additional experiment done afterwards showed that when males of *P. thoas* were removed from the hilltop, territories of *B. polydamas* were also set up in area III (Fig. 1B). Landmarks like the highest point, trees and small plants were used by both species as reference points for territory boundaries.

Territories of *E. orthosilaus* did not overlap with the other species. They were set up to form a barrier to newly arriving butterflies at the hilltop. These butterflies hovered or patrolled continuously several meters above the canopy of the larger trees, which were used as central reference points in their territories.

In all cases territories were set up on the north side of the hill, and only pursuing males were observed flying to the south side (Fig. 1, area V). As newly arriving butterflies were always observed coming from the north, it is possible that the formation of territories on this side of the hilltop can be related to the proximity of the forests below the hill, and/or to solar movements.

Discussion

Results support the idea that these swallowtail butterflies are indeed territorial hilltoppers, with territoriality defined in the sense of Brown & Orians (1970). The assembly of males on the hilltop is also similar to the lek behavior of many vertebrate species; see also DeVries (1980) for a Pierine butterfly.

The defense of landmark territories seems to be a common mate-locating tactic among Papilionid butterflies. However, many differences related to site tenacity and aggression toward intruder males have been shown in some well studied species. Males of *Papilio zelicaon* and *P. polyxenes* actively defend hilltop territories to which they return over days or even weeks (Shields, 1967; Lederhouse, 1982). Otherwise males of *Battus philenor* perch on peaks and/or patrol routes along ridgetops but show little site tenacity and interact only briefly with conspecific males (Rutowski et al., 1989). The more aggressive behavior in the genus *Papilio* when compared to *Battus* species was also observed in this work. Territorial preferences and behavioral activities were so similar between *P. thoas* and *B. polydamas* as to lead to interspecific aggression and nonoverlapping territories. *P. thoas* often won aggressive encounters and established its territories in the most disputed sites while *B. polydamas* was compelled to use neighbour areas. Such observations may suggest that interspecific competition for territories played an important role in the evolution of different mate-locating tactics among swallowtail butterflies and even among other hilltopping species, since similarities in male preferences for territories have been shown for many taxa including distantly related species like butterflies and wasps (Alcock & O'Neill, 1987).

Aggressive encounters in adult butterflies, which do not bear any specialised organ or appendix to injure other animals, are often characterized by ritualized flights and chases that rarely lead to contact among individuals as those observed in *P. thoas* and especially in *E. orthosilaus*. This kind of behavior seems to be common in other *Eurytides* species like *E. protesilaus* (Cr., 1707) also present in the region and frequently misled with *E. orthosilaus* when observed at distance.

Territorial hilltopping seems to be density-dependent in swallowtail butterflies since it was never observed when few individuals were present on the hilltop (see Brown et al. 1981 for population dynamics of *B. polydamas* and other troidine swallowtails). The most common behaviors observed in solitary males on the hilltop were extensive patrolling and/or perching near the highest point. In this situation butterflies frequently left early or appeared on the hilltop intermittently.

"Restricted patrolling" and "perching" in these butterflies could be considered as true territorial behaviors. In the case of *P. thoas* and *B. polydamas*, restricted patrolling was more frequently observed when two or more males were together in the area. In two cases, when a male

of *P. thoas* was removed from the territorial site its conspecific neighbor increased its flight area, returning to extensive patrolling again. "Perching" has been also observed in other nonterritorial butterflies and thus cannot be necessarily considered a conspicuous territorial behavior. According to Scott (1986) it occurs because butterfly eyes are better at detecting fluttering movements than detailed shape and color pattern. Butterflies approach animals to smell and see them in order to find out if they be females or males of the same species. On the other hand, in the case of *P. thoas* and *B. polydamas*, aggressive acts always ensue when the passing butterfly is a conspecific male. Under such conditions many authors regard this behavior as territorial (see revision of Fitzpatrick & Wellington, 1983).

The greater behavioral differences found between *E. orthosilaus* and the other species are probably due to the ability of the "kite" swallowtail *E. orthosilaus* to use the wind for gliding or hovering motionless for relatively long periods of time without strong wing movements; therefore perching may not be necessary. *P. thoas* and *B. polydamas* must alternate behaviors like hovering and restricted patrolling with resting on some projection, since these behaviors are more expensive energetically due to the strong wing movements required.

Mating success of hilltopping males seemed to be small. Matings were not observed during several full day observation sessions and did not occur during scan sampling periods. A relatively low mating frequency has been also reported for other hilltopping invertebrates (Alcock, 1981; 1987). According to Shields (1967) matings are rarely observed because females of many species of hilltopping butterflies generally mate only once or a few times. For at least one hilltopping swallowtail butterfly, *P. polyxenes*, it was observed that most matings occurred in territories placed in small elevations in the area (Lederhouse, 1982).

Acknowledgments. I thank J.V.C. Ortiz, O.A. Shibatta, S.O. Ferreira, N.F. Martins, G.C. Dalton and B.F. Dias for assistance in the field. K.S. Brown Jr., P.J. DeVries and an "anonymous" reviewer read drafts of the manuscript and furnished many helpful comments. Field facilities were provided by Eletronorte.

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